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Can Pallars i Llobateres: A new hominoid-bearing locality from the late Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula)

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ABSTRACT

In the Iberian Peninsula, Miocene apes (Hominoidea) are generally rare and mostly restricted to the Vallès-Penedès Basin. Here we report a new hominoid maxillary fragment with M^2 from this basin. It was surface-collected in March 2017 from the site of Can Pallars i Llobateres (CPL, Sant Quirze del Vallès), where fossil apes had not been previously recorded. The locality of provenance (CPL-M), which has delivered no further fossil remains, is located very close (ca. 50 m) to previously known CPL outcrops, and not very far (ca. 500 m in NW direction) from the classical hominoid-bearing locality of Can Poncic 1. Here we describe the new fossil and, based on the size and proportions of the M^2 , justify its taxonomic attribution to *Hispanopithecus* cf. *laietanus*, a species previously recorded from several Vallesian sites of the Vallès-Penedès Basin. Based on the associated mammalian fauna from CPL, we also provide a biochronological dating and a paleoenvironmental reconstruction for the site. The associated fauna enables an unambiguous correlation to the *Cricetulodon hartenbergeri* – *Progonomys hispanicus* interval local subzone, with an estimated age of 9.98–9.73 Ma (late Vallesian, MN10). Therefore, CPL-M is roughly coeval with the *Hispanopithecus laietanus*-bearing localities of Can Llobateres 1 and Can Feu 1, and minimally older than those of La Tarumba 1 and Can Llobateres 2. In contrast, CPL-M is younger than the early Vallesian (MN9) localities of Can Poncic 1 (the type locality of *Hispanopithecus crusafonti*) as well as Polinyà 2 (Gabarró) and Estació Depuradora d'Aigües Residuals –Riu Ripoll 13, where *Hispanopithecus* sp. is recorded. The associated fauna from CPL indicates a densely forested and humid paleoenvironment with nearby freshwater. This supports the view that *Hispanopithecus* might have been restricted to dense wetland forests soon before its extinction during the late Vallesian, due to progressive climatic deterioration. Coupled with the existence of other fossiliferous outcrops in the area, this find is most promising for the prospect of discovering additional fossil hominoid remains in the future.

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1. Introduction

1.1. The hominoid find from Can Pallars i Llobateres

Miocene apes (Primates: Hominoidea) from Iberia are geographically restricted to Catalonia (NE Iberian Peninsula), mostly coming from multiple sites in the Vallès-Penedès Basin (Alba, 2012), near Barcelona (Casanovas-Vilar et al., 2016a). Although several partial hominoid skeletons have been recovered there (Moyà-Solà and Köhler, 1996; Moyà-Solà et al., 2004; Alba, 2012; Alba et al., 2012b, 2015), hominoid remains are generally scarce and mostly consist of isolated specimens, being considered 'rare' or uncommon taxa that require a large sampling effort to be adequately documented (e.g., Alba, 2012; Alba et al., 2017a). This notwithstanding, sometimes hominoid finds are the result of fortunate circumstances (e.g., the partial skeleton of *Hispanopithecus laietanus* from Can Feu 1; Alba et al., 2012b). Here we report a maxillary fragment from the site of Can Pallars i Llobateres² (CPL, Sant Quirze del Vallès; Llenas Avellaneda, 1999; Furió et al., 2015; Casanovas-Vilar et al., 2016a,b), which was surface-collected by J. Manel Méndez in March 2017. We describe and figure this specimen, and compare it with previously known hominoid remains from the Vallès-Penedès Basin, in order to justify its taxonomic assignment. Based on the study of the unpublished associated vertebrate fauna, we further contextualize this find from both chronological and paleoenvironmental viewpoints.

1.2. Can Pallars i Llobateres

CPL is located ca. 500–600 m NW from the site of Can Poncic³ (CP, Sant Quirze del Vallès; Crusafont Pairó and Truyols Santonja, 1947; Figs. 1 and 2). The exact location of CP localities (Crusafont Pairó and Golpe Posse, 1972; Golpe Posse, 1974) is uncertain due to the insufficient published documentation (Crusafont Pairó and Truyols Santonja, 1947; Santafé Llopis, 1978; Llenas i Avellaneda, 1996). However, based on published photographs (Crusafont Pairó and Truyols Santonja, 1947), orthophotos from 1946 (ICGC, 2017), and recent surveys (Alba and Almécija, 2017), CP can be confidently located within an area of about 0.7 ha (Fig. 2). Hominoid remains were recovered at the locality of Can Poncic 1 (CP1) from the early 1950s to the early 1970s (Crusafont Pairó, 1958; Crusafont Pairó and Hürzeler, 1969; Crusafont-Pairó and Golpe-Posse, 1973; Moyà-Solà et al., 1990; Harrison, 1991; Golpe Posse, 1993; Alba, 2012; Alba et al., 2012a, 2013; Pérez de los Ríos et al., 2013). CP1 is the type locality of the extinct great ape *Hispanopithecus crusafonti* (Begun, 1992), otherwise only recorded from Teulera del Firal (Begun, 1992; Alba, 2012) in the Seu d'Urgell Basin (Catalan Pyrenees).

The site of CPL was discovered in 1999, when urbanization works unearthed several Miocene large mammal remains within an area smaller than 1.5 ha (Fig. 2). These were excavated by a team from the former Institut de Paleontologia M. Crusafont in Sabadell (IPS), which also screen-washed some sediment samples. The exact provenance of most remains was not documented, but those subsequently surface-collected came from different spots (Fig. 2): CPL-A, CPL-B, CPL-P1 (=CPL-C), CPL-P3, CPL-P2, and CPL-P4. The more abundant small mammal material came from two consecutive stratigraphic horizons (CPL s.s. and CPL3) within the classical CPL area (M. Llenas Avellaneda, pers. comm. to D.M.A.; see also Llenas Avellaneda, 1999). Except for a provisional faunal list provided in the field report (Llenas Avellaneda, 1999)

and a few subsequent emendations (Casanovas-Vilar et al., 2016b), the fossils from CPL remained mostly unpublished (but see Furió et al., 2015). The hominoid maxillary fragment described here was found embedded within a small sediment block of carbonated claystone in locality CPL-M (Alba et al., 2017b), within an uncultivated land parcel (Fig. 2) very close to the classical CPL outcrops (roughly equivalent to CPL-B). The find was immediately reported to the Archaeological and Paleontological Survey of the Generalitat de Catalunya, and is currently housed at the Institut Català de Paleontologia Miquel Crusafont (ICP) with catalog No. IPS102942.

2. Materials and methods

2.1. Comparisons with other hominoids

IPS102942 was compared with upper molars of other Vallès-Penedès dryopithecines (Begun et al., 1990; Begun, 1992; Golpe Posse, 1993; Moyà-Solà and Köhler, 1995, 1996; Moyà-Solà et al., 2004, 2009a,b; Alba, 2012; Alba et al., 2012a, 2013; Pérez de los Ríos et al., 2013), with particular emphasis on those from CP1 (*H. crusafonti*) and Can Llobateres 1 and 2 (CLL1 and CLL2, respectively; tooth locus identifications of *H. laietanus* from CLL1 after Alba et al., 2012a). No upper molars are available from the other Vallès-Penedès localities with *H. laietanus*, namely: La Tarumba 1 (LT1, type locality; Villalta Comella and Crusafont Pairó, 1944; Golpe Posse, 1993), Polinyà 2 (Gabarró; PO2; Crusafont-Pairó and Golpe-Posse, 1973; Golpe Posse, 1993), Estació Depuradora d'Aigües Residuals—Riu Ripoll 13 (EDAR13; Checa Soler and Rius Font, 2003) and Can Feu 1 (CF1; Alba et al., 2012b). All specimens were measured with digital calipers to the nearest 0.1 mm by one of the authors (D.M.A.). The following measurements were taken: BL, buccolingual breadth (in mm, taken both at the mesial and the distal crown portions); MD, mesiodistal length (in mm); and BLI, breadth/length index (in %, computed as maximum BL/MD × 100). Dental terminology follows Alba et al. (2013:Fig. 1).

2.2. Associated fauna

Large vertebrate remains from CPL are very scarce, including 52 specimens from CPL, CPL-B, CPL-A, CPL-P1, CPL-P3 and CPL-P4—see Supplementary Online Material (SOM) S1 for further details. The associated small mammal fauna is represented by a collection of 384 micromammal teeth from CPL and CPL3 (see SOM S1). All of the fossils are housed at the ICP.

2.3. Coordinates

Geographic coordinates for paleontological localities are given in the Universal Transverse Mercator (UTM) system, based on the European Terrestrial Reference System 1989 (ETRS89). They were verified with the aid of topographic maps and orthophotos from the web application VISSIR v3.26 of the Institut Cartogràfic i Geològic de Catalunya (ICGC, 2017).

3. Results

3.1. Description of the hominoid maxilla

IPS102942 is a left maxillary fragment (ca. 1.5 × 2.0 cm), still partially embedded in matrix, that preserves an alveolus with broken roots and a socketed molar crown (Fig. 3A–C). The specimen is poorly preserved, displaying multiple diagenetic cracks filled with sediment. Given the poor preservation, little can be said about the comparative anatomy of the maxilla, although the

² Formerly spelled 'Can Pallàs de Llobateres' or 'Can Pallars de Llobateres.'

³ Formerly spelled 'Can Poncic' or 'Can Ponsich.'

position of the preserved portion of the palatine process relative to the alveolar margin suggests that the palate was deep.

Alba et al. (2017b) originally identified the near-complete, socketed tooth as M^1 , but closer examination suggests it is M^2 . The missing crown, anterior to the molar crown, is broken at or slightly below the cervix. The lingual root of this tooth, visible along most of its length (because the maxillary bone lacks its lingual side), is mesiodistally broad and resembles the single fused root of the socketed molar (which is slightly exposed below the cervix). The cross-section of the roots close to the alveolar plane, in occlusal view, reveals two buccal root canals, indicating that two distinct buccal roots were likely present, as is typical of hominoid upper molars. Although the presence of one or two buccal roots in hominoid P^4 is variable (Emonet and Kullmer, 2014), the aforementioned morphology of the lingual root enables us to rule out an identification of the missing crown as a P^4 , meaning that the missing crown is a molar. Given that the well-developed metacone and only moderate distal tapering of the molar crown are not consistent with an M^3 , the socketed molar must belong to an M^2 , and the missing crown was an M^1 .

The molar crown is well preserved, except for a missing enamel chip that would have included the lingual and distal aspects of the hypocone, as well as most of the distal marginal ridge—which nevertheless does not preclude taking reliable crown measurements. The crown is quite worn, with extensive dentine exposure at the protocone and the preserved portion of the hypocone. It displays a subrectangular to suboval and distally tapering occlusal contour, being buccolingually broader (BL = 9.8 mm) than mesiodistally long (estimated MD = 8.7 mm; BLI = 112.6%), and much broader on the mesial than on the distal (BL = 8.7 mm) portions of the crown. The mesial contour of the crown is rather straight, whereas the buccal and distal contours are convex, and the lingual contour is more clearly biconvex. The crown displays quite vertical walls and is not particularly inflated toward its base. There are four main cusps, the protocone being the most extensive, the hypocone being the smallest, and the paracone and metacone being similar in size to one another (although the former is somewhat higher). The buccal cusps are more mesially located than the corresponding lingual cusps, and very peripheral. The hypocone is located on the distolingual corner of the crown. Mesio buccally from the protocone, at approximately the crown midline behind the mesial marginal ridge, there is a small dentine exposure that seemingly represents a completely worn protoconule located at the end of the similarly worn preprotocrista. A short and slit-like mesial fovea is still discernible on the buccal moiety of the crown in spite of wear. This fovea, which originally likely ran to the protoconule base, is distally delimited by a rather straight and transverse hypoparacrista directed toward the former protoconule. Two occlusal grooves can still be observed in spite of wear: a transverse one, separating the bases of the protocone and the hypocone, and a more obliquely oriented one, which runs from the buccal crown wall to the center of the trigon basin, separating the bases of the paracone and the metacone, and further transecting the merging point of the long postparacrista with the shorter premetacrista. The postmetacrista and the preparacrista progressively curve in a lingual direction until merging with the distal and mesial marginal ridges, respectively. A straight crista obliqua apparently linked the protocone with the metacone, although the postprotocrista portion has been completely obliterated by wear. Similarly, a somewhat developed hypocone-metacone crista might have crossed the distal fovea, although it has been largely obscured by wear and it is not possible to ascertain whether it would have been continuous or not. No secondary enamel folds or wrinkling can be discerned, but this might be simply attributable to wear. No buccal or lingual cingular remnants are present.

3.2. Comparisons with other Vallès-Penedès hominoids

Compared with the available M^1 and M^2 sample of Vallès-Penedès hominoids, IPS102942 (Fig. 4a) fits well with the occlusal morphology of previously known specimens of *Hispanopithecus* spp. (Fig. 4b–h,k–p). In particular, like the specimens of *Hispanopithecus* (Alba et al., 2013; Pérez de los Ríos et al., 2013), IPS102942 differs from the upper molars of the middle Miocene taxa—*Dryopithecus* (Fig. 4i), *Pierolapithecus* (Fig. 4j), and *Anoiapithecus* (Fig. 4q–s)—in the more peripheralized cusps, the less bulging crown base, the apparently lesser developed metacone-hypocone crista (even if blurred by wear in IPS102942), and the more reduced cingula (although their development is variable in *Hispanopithecus*; Alba et al., 2012b). Compared to the two species of *Hispanopithecus* from the Vallès-Penedès, the slightly tapering occlusal profile of IPS102942 more closely resembles that of the M^2 (Fig. 4e–g,k,n–p) than the squarer profile of the M^1 (Fig. 4b–f, k–m), even though IPS102942 appears smaller and mesiodistally shorter than the previously recorded M^2 . The hypocone in IPS102942 appears mesiodistally aligned with the protocone, as in the M^2 of *H. laietanus* (Fig. 4f–h), whereas in the M^2 of *H. crusafonti* (Fig. 4k, n) the hypocone is more lingually situated relative to the protocone, as in the M^2 of *Anoiapithecus* (Fig. 4r,s).

With regard to metric comparisons, IPS102942 more closely resembles in both size and proportions the smaller (presumably female) M^1 of *H. laietanus* (Fig. 5a), being somewhat smaller than all available M^2 (Fig. 5b). Thus, the MD (8.7 mm) and BL (9.7 mm) of IPS102942 fall somewhat below the known M^2 size ranges of both *H. laietanus* (MD mean = 10.18 mm, range = 8.8, 11.2 mm; BL mean = 11.18 mm, range = 10.0, 11.6 mm; $n = 5$) and *H. crusafonti* (MD mean = 10.10 mm, range = 8.8, 11.1 mm; BL mean = 11.50 mm, range = 10.9, 12.2 mm; $n = 4$; data from Alba et al., 2012a:Table 4). In turn, the BLI (112.6%) of IPS102942 falls well within the M^2 range of both *H. laietanus* (BLI mean = 110.54%, range = 101.8%, 130.7%; $n = 5$) and *H. crusafonti* (BLI mean = 114.58%, range = 105.4%, 127.3%; $n = 4$; data from Alba et al., 2012a:Table 4).

4. Discussion

4.1. Taxonomic assignment

Even before the erection of *H. crusafonti* by Begun (1992), the distinction of the CP1 hominoid sample at the species rank advocated by Begun et al. (1990) was already controversial (Harrison, 1991; Ribot et al., 1996; Andrews et al., 1996). However, the taxonomic validity of *H. crusafonti* has been subsequently supported by multiple researchers (e.g., Cameron, 1999; Begun, 2002, 2009; 2015; Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011; Pickford, 2012; Alba, 2012; Alba et al., 2012a). Alba et al. (2012a) concurred with Ribot et al. (1996) that the development of upper molar cingula is too variable to be diagnostic (contra Begun, 1992, 2002), but confirmed that *H. crusafonti* tends to display broader M^1 and M^2 than *H. laietanus* (Begun, 1992, 2002). However, based on the available sample, such differences in occlusal proportions are only significant for the M^1 (Alba et al., 2012a), so that this diagnostic criterion is not useful in the case of IPS102942, which moreover falls in the extensive overlap zone between the two species. This notwithstanding, an assignment to *H. laietanus* is supported by some subtleties of occlusal morphology (hypocone position), for which *H. crusafonti* differs from *H. laietanus* and more closely approaches the condition of *Anoiapithecus* (see Alba et al., 2013). Additional remains—the I^1 is particularly diagnostic (Begun, 1992; Alba et al., 2012a)—would be required to further substantiate the attribution of IPS102942 to *H. laietanus*. Given that

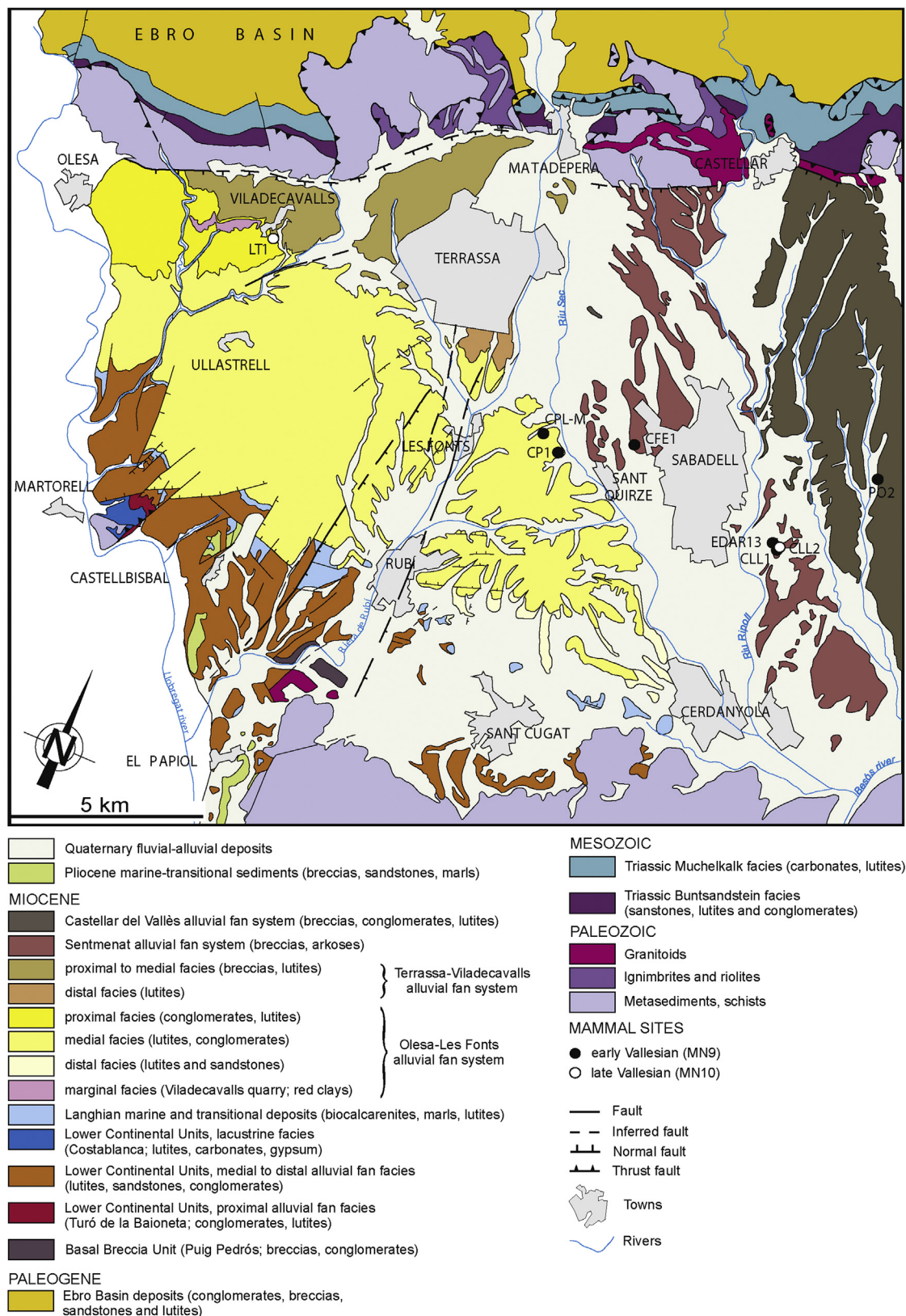


Figure 1. Geological map of the Vallès sector of the Vallès-Penedès Basin (NE Iberian Peninsula), indicating the location of all the Vallesian localities that have delivered fossil remains of *Hispanopithecus* spp. Abbreviations (municipalities indicated within brackets): CFE1 = Can Feu 1 [Sant Quirze del Vallès]; CLL1 = Can Llobateres 1 [Sabadell]; CLL2 = Can Llobateres 2 [Sabadell]; CP1 = Can Poncic 1 [Sant Quirze del Vallès]; CPL-M = Can Pallars i Llobateres-M [Sant Quirze del Vallès]; EDAR13 = Estació Depuradora d'Aigües Residuals—Riu Ripoll 13 [Sabadell]; LT1 = La Tumba 1 [Viladecavalls]; PO2 = Polinyà 2 [Polinyà].



Figure 2. Aerial photograph showing various fossiliferous outcrops from Can Pallars i Llobateres (CPL) and the approximate location of the classical site of Can Poncic (CP). Dotted white rectangles denote loosely defined sites, whereas red asterisks denote the exact location of paleontological localities. The location of the Can Poncic farmhouse and other local toponyms are also indicated. North is toward the top. Coordinates are indicated below (for details on the system of geographical coordinates used, please see the [Materials and methods](#)). Legend: CPL = Can Pallars i Llobateres (central coordinates: 31N 421450 E–4598750 N, including CPL-A and CPL3); CPL-M (=CPL-B) = Location of the hominoid find by Méndez (31N 421380 E–4598702 N); CPL-P2 = Spot 2 of CPL (31N 421610 E–4598607 N); CPL-P3 = Spot 3 of CPL (31N 421423 E–4598424 N); CPL-P4 = Spot 4 of CPL (31N 421672 E–4598609 N); CP = Can Poncic (approximate coordinates 31N 421900 E–4598475 N). Other CPL localities not depicted in the figure include CPL-B (31N 421410 E–4598675 N) and CPL-P1 (=CPL-C; 31N 421470 E–4598485 N). Figure modified from base orthophotos downloaded from VISSIR v3.26 (ICGC, 2017; sheets 286–119 and 287–119, scale 1:2500), ©Institut Cartogràfic i Geològic de Catalunya, with permission allowed by licence Creative Commons (CC) – Attribution 4.0 International (CC BY 4.0; see <http://www.icgc.cat/Ajuda/Avis-legal> for the reuse policies allowed for ICGC web contents).

a single tooth is available, we prefer to be cautious and provide a tentative assignment to this species, i.e., *H. cf. laietanus*.

4.2. Age

An updated faunal list from CPL is reported in [Table 1](#) (see also [SOM S2](#) and [SOM Figs. S1–S2](#)). The presence of the three-toed horse *Hippotherium* conclusively demonstrates the Vallesian age of CPL, being first recorded in the Vallès-Penedès Basin at 11.2 Ma ([Agustí et al., 1997](#); [Garcés et al., 1997, 2003](#); [Casanovas-Vilar et al., 2016a,b](#)). This agrees with the presence of the boselaphin antelope *Miotragocerus* aff. *pannoniae* sensu [Moyà-Solà \(1983\)](#) and the lagomorph *Prolagus crusafonti*, which apparently replaced *Miotragocerus monnacensis* ([Moyà-Solà, 1983](#); [Fuss et al., 2015](#)) and *Prolagus oeningensis* ([López Martínez, 2001](#); [Angelone and Veitschegger, 2015](#)), respectively, in the Vallesian. Rodents ([Fig. 6](#)) and insectivores enable a more precise dating, the assemblage being dominated by *Cricetodon sabadellensis*, as in other Vallesian hominoid-bearing localities (CLL1 and CFE1; [Casanovas-Vilar et al., 2012](#)). The presence of this species (instead of its putative ancestor, *Cricetodon hartenbergeri*), coupled with that of *Democricetodon* cf. *nemoralis* and *Keramidomys pertesunatoi*, and the absence of *Progonomys hispanicus*, indicates an unambiguous correlation to the *C. hartenbergeri* – *P. hispanicus* interval local subzone of the Vallès-Penedès Basin ([Casanovas-Vilar et al., 2011, 2012; 2016a,b](#)), with an estimated age of 9.98–9.73 Ma ([Casanovas-Vilar et al., 2016a,b](#)). This is consistent with the presence of *Dinosorex* (which

became extinct in the Vallès-Penedès Basin shortly after the MN9/MN10 transition; [Furió et al., 2015](#)) and the co-occurrence between *Lantanotherium sanmigueli* and *Crusafontina endemica* (characteristic of this subzone; [Casanovas-Vilar et al., 2012](#)).

CPL is therefore roughly coeval with CFE1 (same subzone; [Casanovas-Vilar et al., 2012, 2016a,b](#)) and CLL1 (with a magnetostratigraphically interpolated age of 9.76 Ma; [Agustí et al., 1996](#), updated by [Casanovas-Vilar et al., 2016b](#) after new chron boundaries in [Hilgen et al., 2012](#)), where *H. laietanus* is also recorded ([Crusafont Pairó, 1958, 1965](#); [Crusafont Pairó and Hürzeler, 1969](#); [Crusafont-Pairó and Golpe-Posse, 1973](#); [Begun et al., 1990](#); [Moyà-Solà et al., 1990](#); [Harrison, 1991](#); [Golpe-Posse, 1993](#); [Alba, 2012](#); [Alba et al., 2012a,b](#)). Because of the absence of *Progonomys*, these localities have been classically correlated to MN9 (early Vallesian; e.g., [Agustí et al., 1996, 1997](#); [Furió et al., 2015](#); [Casanovas-Vilar et al., 2011, 2012, 2016a](#))—unlike the slightly younger locality of CLL2, which has also yielded remains of *H. laietanus* ([Moyà-Solà and Köhler, 1993, 1995, 1996](#); [Almécija et al., 2007](#); [Alba, 2012](#)) and is correlated to the *C. sabadellensis* + *P. hispanicus* concurrent range subzone (i.e., to MN10, late Vallesian), with an interpolated age of 9.62 Ma (updated by [Casanovas-Vilar et al., 2016b](#), after [Agustí et al., 1996](#)). Under the ‘faunal’ concept of MN units, CLL1 was even selected by some authors ([Fahlbusch, 1976](#); [De Bruijn et al., 1992](#); [Mein, 1999](#)) as the reference locality for MN9. However, *Progonomys* already commonly occurs in roughly coeval sites from other Iberian basins ([Hilgen et al., 2012](#); [Van Dam et al., 2014](#); [Casanovas-Vilar et al., 2016b](#)), with the lower boundary of MN10 being set at

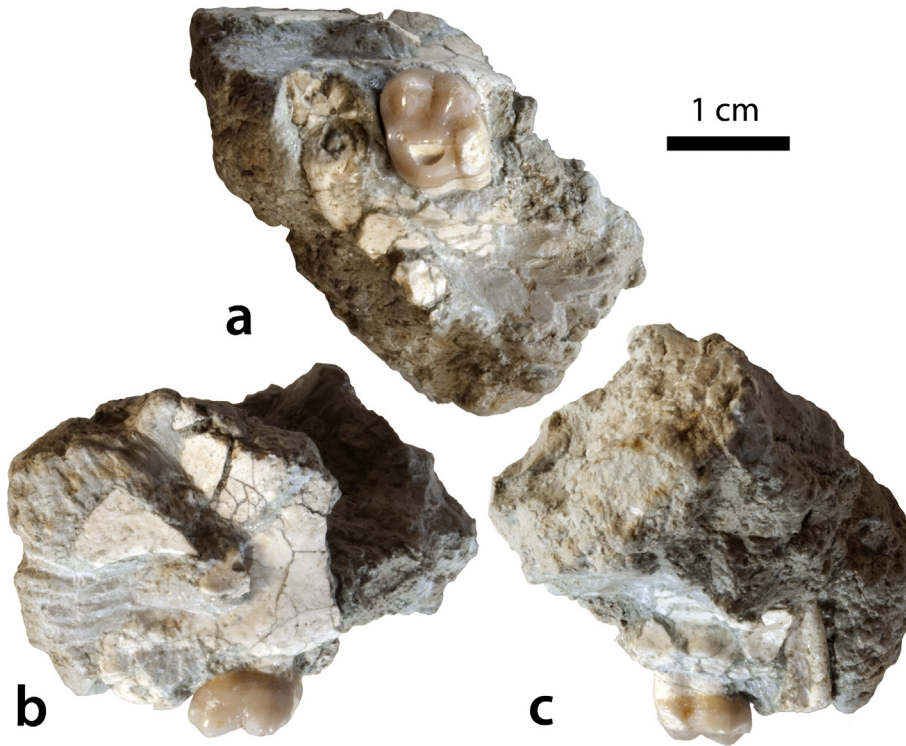


Figure 3. Left maxillary fragment with M² (IPS102942) of *Hispanopithecus* cf. *laietanus* from CPL-M in occlusal (a), buccal (b) and lingual (c) views.

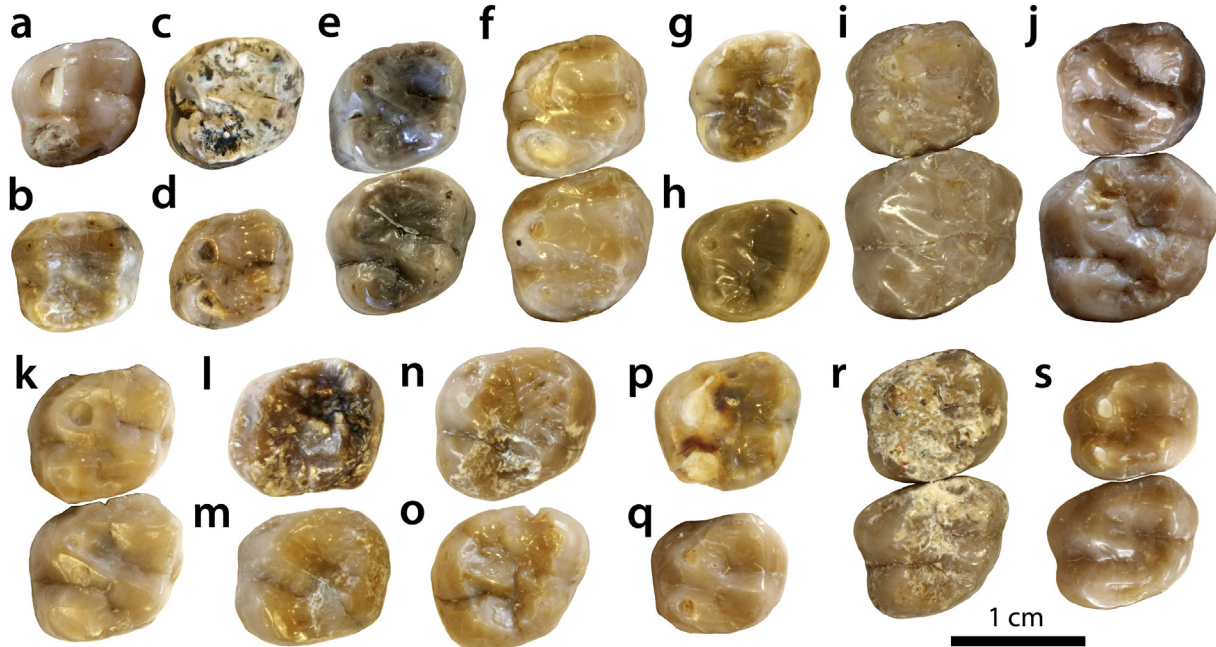


Figure 4. Comparison of the occlusal morphology of the left M² (IPS102942) of *Hispanopithecus* cf. *laietanus* from CPL-M (a) with the M¹ and/or M² of other Vallès-Penedès hominoids: b) left M¹ (IPS1781) of *H. laietanus* from CCL1; c) right M¹ (IPS1844, reversed) of *H. laietanus* from CLL1; d) left M¹ (IPS1788) of *H. laietanus* from CLL1; e) left M¹–M² (IPS58338–IPS58339) of *H. laietanus* from CCL1; f) right M¹–M² (IPS18000.5) of *H. laietanus* from CLL2; g) left M² IPS1794 of *H. laietanus* from CLL1; h) left ?M² (IPS1771) of *H. laietanus* from CLL1; i) left M¹–M² (IPS35026) of *Dryopithecus fontani* from ACM/C3-Ae; j) left M¹–M² (IPS21350, holotype) of *Pierolapithecus catalaunicus* from ACM/BCV1; k) left M¹–M² (IPS1798, holotype) of *Hispanopithecus crusafonti* from CP1; l) left M¹ (IPS1815) of *H. crusafonti* from CP1; m) left M¹ (IPS1818) of *H. crusafonti* from CP1; n) left M² (IPS1820) of *H. crusafonti* from CP1; o) right M³ or M² (IPS1812, reversed) of *H. crusafonti* from CP1; p) right M² (IPS1821, reversed) of *H. crusafonti* from CP1; q) left M¹ (IPS41712) of *Anoiapithecus brevirostris* from ACM/C3-Aj; r) left M¹–M² (IPS43000, holotype) of *A. brevirostris* from ACM/C3-Aj; s) right M¹–M² (IPS35027, reversed) of *A. brevirostris* from ACM/C1-E*. Locality abbreviations: ACM = Abocador de Can Mata (els Hostalets de Pierola); C1 = Cel·la 1 (ACM sector); C3 = Cel·la 3 (ACM sector); for other abbreviations, see Figure 1 caption.

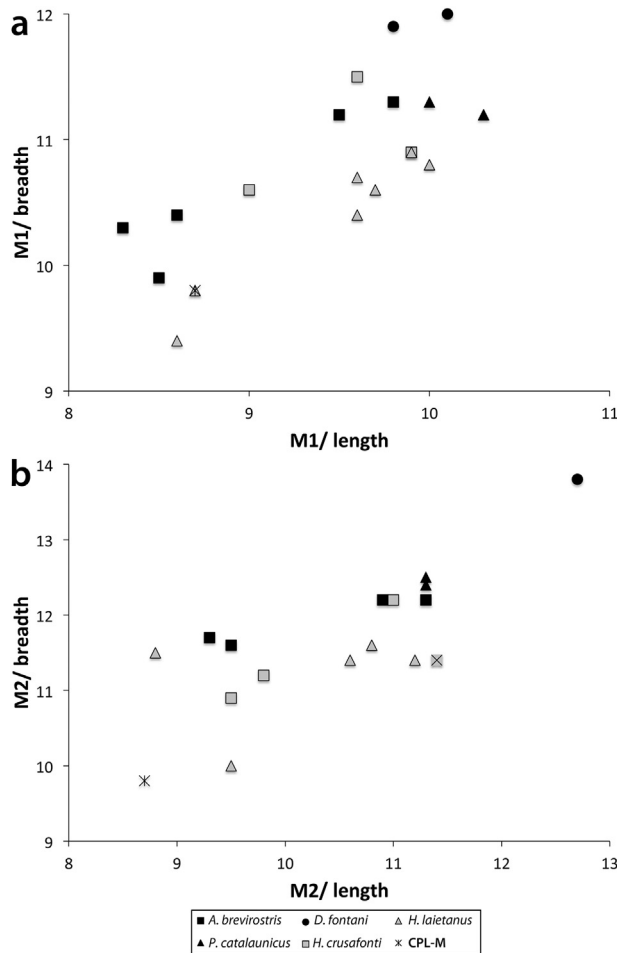


Figure 5. Bivariate plots of buccolingual breadth (BL, in mm) vs. mesiodistal length (MD, in mm) of the M¹ (IPS102942) of *Hispanopithecus* cf. *laietanus* from CPL-M, as compared to the M¹ (a) and M² (b) of Vallès-Penedès hominoids.

9.98 Ma. Therefore, under a strictly biostratigraphic approach to MN units, MN10 would include the local subzone to which CPL, CLL1 and CFE1 are correlated (Casanovas-Vilar et al., 2016b).

The latest occurrence of *H. laietanus* corresponds to its type locality (LT1; Villalta Comella and Crusafont Pairó, 1944; Golpe Posse, 1993; Alba, 2012), correlated to the local *Rotundomys montisrotundi* lineage subzone (MN10) and with a magnetostratigraphically interpolated age of 9.57 Ma (Casanovas-Vilar et al., 2016a). In turn, the oldest possible occurrence of *Hispanopithecus* in the basin is documented at PO2 and EDAR13 (Crusafont-Pairó and Golpe-Posse, 1973; Golpe Posse, 1982, 1993; Moyà Solà et al., 1990; Harrison, 1991; Begun, 2002; Checa Soler and Rius Font, 2003; Alba, 2012). The former is correlated to MN9 in a strict sense (11.2–10.0 Ma; Casanovas-Vilar et al., 2011, 2016a), whereas EDAR13 is correlated to the *C. hartenbergeri* range subzone (10.3–9.98 Ma; Casanovas-Vilar et al., 2011, 2016a,b) and therefore older than CLL1. Even though the material from PO2 and EDAR13 has been classically assigned to *H. laietanus* (Crusafont-Pairó and Golpe-Posse, 1973; Golpe Posse, 1982, 1993; Moyà Solà et al., 1990; Harrison, 1991; Ribot et al., 1996; Checa Soler and Rius Font, 2003; Casanovas-Vilar et al., 2011; Alba, 2012), the scarce available remains are arguably undiagnostic at the species level: the female C¹ from PO2 was assigned to *H. laietanus* based on its similarities to those from CLL1 (Crusafont-Pairó and Golpe-Posse, 1973; Golpe Posse, 1982, 1993), but this tooth type is unknown for *H. crusafonti* (e.g., Begun,

Table 1

Updated list of the faunal assemblage from Can Pallars i Llobateres (CPL, including those small mammal specimens labelled as CPL3, as well as the large mammal specimens from CPL, CPL-A, CPL-B, CPL-P1, CPL-P3, CPL-P4 and CPL-M).

Order	Family	Taxonomic assignment
Testudines	Geoemydidae	<i>Ptychogaster</i> sp.
Testudines	Testudinidae	<i>Testudo</i> sp.
Testudines	Testudinidae	<i>Titanochelon</i> cf. <i>richardi</i>
Squatama	Indet.	Serpentes indet.
Primates	Hominidae	<i>Hispanopithecus</i> cf. <i>laietanus</i>
Proboscidea	Indet. ^a	Proboscidea indet. ^a
Artiodactyla	Cervidae	Cervidae indet.
Artiodactyla	Bovidae	<i>Miotragocerus</i> aff. <i>pannoniae</i>
Perissodactyla	Equidae	<i>Hippotherium</i> (<i>primigenium</i>) cf. <i>catalaunicum</i> ^b
Perissodactyla	Rhinocerotidae	Rhinocerotidae indet.
Eulipotyphla	Soricidae	<i>Crusafontina</i> <i>endemica</i>
Eulipotyphla	Erinaceidae	<i>Lantanothereum</i> <i>sanmigueli</i>
Eulipotyphla	Heterosoricidae	<i>Dinosorex</i> <i>grycivensis</i>
Eulipotyphla	Dimylidae	<i>Plesiodymulus</i> <i>chantrei</i>
Eulipotyphla	Talpidae	<i>Talpa</i> <i>minuta</i>
Lagomorpha	Ochotonidae	<i>Prolagus</i> <i>crusafonti</i>
Rodentia	Cricetidae	<i>Cricetodon</i> <i>sabadellensis</i>
Rodentia	Cricetidae	<i>Eumyarion</i> <i>leemanni</i>
Rodentia	Cricetidae	<i>Democricetodon</i> cf. <i>memoralis</i>
Rodentia	Cricetidae	<i>Hispanomys</i> <i>thaleri</i>
Rodentia	Cricetidae	<i>Anomalomys</i> <i>gaillardi</i>
Rodentia	Eomyidae	<i>Eomyops</i> <i>catalaunicus</i>
Rodentia	Eomyidae	<i>Keramidomys</i> <i>pertesunatoi</i>
Rodentia	Gliridae	<i>Muscardinus</i> <i>hispanicus</i>
Rodentia	Gliridae	<i>Muscardinus</i> <i>vallesiensis</i>
Rodentia	Gliridae	<i>Glirulus</i> <i>lissiensis</i>
Rodentia	Gliridae	<i>Paragilulus</i> <i>werenfelsi</i>
Rodentia	Gliridae	<i>Myoglis</i> <i>meini</i>
Rodentia	Sciuridae	<i>Spermophilinus</i> <i>bredai</i>
Rodentia	Sciuridae	<i>Heteroxerus</i> <i>grivensis</i>
Rodentia	Castoridae	<i>Euroxonomys</i> <i>minutus</i>

^a Llenas Avellaneda (1999) mentioned the recovery of a cervical vertebra of *Tetralophodon longirostris*, but we were unable to find such a material. All the available proboscidean remains from CPL localities are too fragmentary to enable their identification even at the family rank.

^b Following Bernor et al. (1996), we consider *Hippotherium* (*primigenium*) as a species complex (as denoted by the name interpolated within parentheses; see ICZN, 1999:Art. 6.2).

1992), and the same applies to the fragmentary manual phalanges from EDAR13 (Checa Soler and Rius Font, 2003), even if they resemble those of *H. laietanus* from CLL2 (Moyà-Solà and Köhler, 1996; Almécija et al., 2007).

If the PO2 and EDAR13 remains are removed from the hypothesis of *H. laietanus* and assigned to *Hispanopithecus* sp. (contra Alba, 2012), the known stratigraphic range of *H. laietanus* is circumscribed to ca. 10 to 9.57 Ma. This is younger than CP1—the type locality of *H. crusafonti* (Begun, 1992; Alba, 2012; Alba et al., 2012a), correlated with the *C. hartenbergeri* range subzone (10.30–9.98 Ma; Casanovas-Vilar et al., 2016a,b)—suggesting that *H. laietanus* might have postdated *H. crusafonti*. Unfortunately, the lack of diagnostic remains from EDAR13 (roughly coeval to CP1) and dating uncertainties for PO2 do not allow us to conclusively discard some overlap between the stratigraphic ranges of *H. crusafonti* and the younger *H. laietanus* during the latest early Vallesian (MN9).

4.3. Paleoenvironment

Based on its postcranial morphology (Moyà-Solà and Köhler, 1996; Almécija et al., 2007, 2013, 2015; Alba et al., 2010; Alba, 2012; 2012b; Pina et al., 2012) and microwear analyses (Ungar, 1996; DeMiguel et al., 2014), *H. laietanus* can be considered an arboreal orthograde primate with specific adaptations to below-

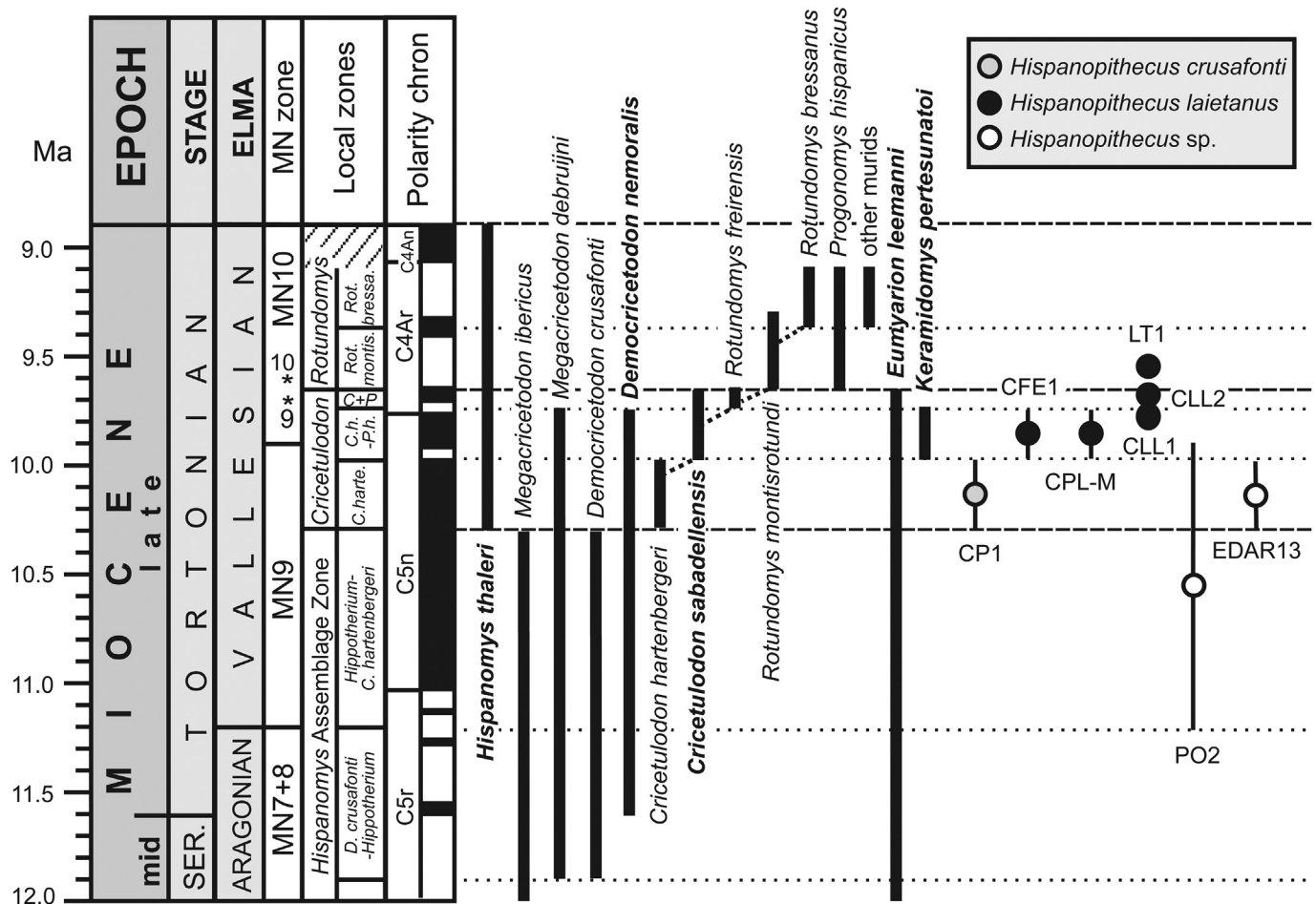


Figure 6. Stratigraphic ranges of the biochronologically most significant rodent species and situation of the Vallès-Penedès localities that have previously yielded fossil remains of *Hispanopithecus*. Rodent species present at CPL-M are indicated in bold. Dashed lines between rodent species indicate phylogenetic relationships. Local biozonation of the Vallès-Penedès Basin is after Casanovas-Vilar et al. (2016b) while Neogene timescale follows Hilgen et al. (2012). In the case of MN (Mammal Neogene) zones, their boundaries are indicated as defined by selected first appearance events (after Hilgen et al., 2012). The reference sites for MN9 (CLL1) and MN10 (Masía del Barbo, Spain) are denoted with asterisks. Note that CLL1 is herein placed within MN10 when MN zones are defined according to first appearance events. For locality abbreviations, see Figure 1 caption. Other abbreviations: C. harten. = *Cricetodon hartenbergeri* range subzone; C. h. – P. h. = *Cricetodon hartenbergeri* – *Progonomys hispanicus* interval subzone; C + P = *Cricetodon sabadellensis* + *Progonomys hispanicus* concurrent range zone. Rot. montis. = *Rotundomys montisrotundi* lineage subzone; Rot. bressa. = *Rotundomys bressanus* lineage subzone.

branch suspension and frugivory—thereby being indicative of densely forested environments, in agreement with the paleo-environmental evidence provided by the CPL associated fauna (Table 1; SOM S2 and SOM Figs. S1–S2).

The tridactyl horse *Hippotherium* (*primigenium*) does not necessarily indicate an open, grassland habitat, given mesowear evidence that it displayed a wide dietary spectrum (Kaiser et al., 2000; Kaiser, 2003). In contrast, the antelope *Miotragocerus* is considered a browser (Merceron et al., 2007) and semiaquatic animal that inhabited closed and swampy areas (Köhler, 1993). The latter is consistent with the nearby presence of freshwater, as further indicated by the beaver *Euroxenyomys* and the geoemydid turtle *Ptychogaster*. Several small mammals are also indicative of a forested environment, including the remarkable diversity of arboreal dormice, the presence of two eomyids, and the more abundant cricetids *Eumyarion* and *Anomalomys* (Casanovas-Vilar and Agustí, 2007)—the latter interpreted as a burrower that would have preferred moist soils (Casanovas-Vilar and Agustí, 2007). The diverse insectivore assemblage from CPL is similarly indicative of moist and warm conditions, as further shown by the presence *Dinosorex* (a typical forest dweller; Furió et al., 2015), *Talpa* (a burrower linked to constantly humid soils; Furió et al., 2011), *Plesiodimylus* (a malacophagous taxon indicative of an abundant

presence of gastropods; Crespo et al., 2018), and *Lantanotherium* and *Crusafontina* (whose extant relatives are restricted to the rainforests of southeastern Asia).

Most of the small mammal taxa apparently associated with humid forest environments are not recorded in coeval sites from the inner Iberian Peninsula, which during the Vallesian were typically characterized by more arid environments (Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008). This applies to most of the insectivores (with the exception of *Crusafontina*; Furió et al., 2011) and multiple rodent taxa (the eomyids, most of the glirids, and the cricetids *Eumyarion* and *Anomalomys*; Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar et al., 2008). This paleobiogeographical evidence suggests that, during the Vallesian, Vallès-Penedès habitats were moister and more densely forested than other areas of the Iberian Peninsula, thus being closer to those from France and Central Europe, as previously noted for the late Aragonian (Casanovas-Vilar et al., 2008). Such environmental differences would account for the observed geographical distribution of Miocene hominoids in the Iberian Peninsula, being only recorded from the more humid and closed environments from the Vallès-Penedès and Seu d'Urgell basins in NE Iberia (e.g., Alba, 2012).

Based on the associated fauna, the paleoenvironment of CPL can be inferred as a densely forested and humid environment with nearby water, similar to that of CLL1. The latter has further yielded plant remains, which together with the fauna allow us to reconstruct its paleoenvironment as a very humid marshy area with nearby dense wetland forests with some (sub)tropical plant elements (Marmi et al., 2012). The newly reported maxillary fragment of *Hispanopithecus* from CPL-M therefore supports the view that this taxon would have been restricted to forested humid habitats providing a year-round fruit supply (Marmi et al., 2012, and references therein). These habitats apparently persisted in the Vallès-Penedès Basin until the early late Vallesian—even if they were progressively becoming more fragmentary, due to an ongoing trend of climatic deterioration that ultimately presumably led to their extinction (Agustí et al., 2003; Casanovas-Vilar et al., 2011; Marmi et al., 2012; DeMiguel et al., 2014).

5. Summary and conclusions

We describe a new hominoid maxillary fragment with M² recovered from a new locality from the site of CPL, where Miocene apes had not been previously reported. Although CPL is relatively close (500 m) to the type locality of *H. crusafonti* (10.30–9.98 Ma, MN9, early Vallesian), based on occlusal morphology the new find is tentatively assigned to *H. cf. laietanus*. The associated fauna from CPL further indicates a younger age (9.98–9.73 Ma), being roughly coeval with other Vallès-Penedès localities with *H. laietanus* (CLL1 and CFE1), correlated to earliest MN10 (late Vallesian) on biostratigraphic grounds. Although some temporal overlap between the two species cannot be completely ruled out, currently available evidence is consistent with a replacement of *H. crusafonti* by *H. laietanus* close to the MN9/MN10 transition (ca. 10.0 Ma). The associated fauna from CPL indicates a densely forested and humid paleoenvironment with nearby freshwater (as in CLL1), thereby strengthening the view that *Hispanopithecus* might have been restricted to dense wetland forests soon before it went extinct in the late Vallesian. Given the existence of other fossiliferous outcrops in CPL, the find reported here is most promising for the prospect of finding additional fossil hominoid remains in this area.

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Supplementary Online Material

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